

MECHANICAL TRANSMISSION IN A PACINIAN CORPUSCLE. AN ANALYSIS AND A THEORY

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SUMMARY

1. An analysis is made of the transmission of mechanical forces through the Pacinian corpuscle. In particular, forces are analysed which produce pressure differences at the centre of the corpuscle and lead to excitation of the sensory nerve ending.

2. The main structural elements in force transmission through the corpuscle are the lamellae, their interconnexions, and the interlamellar fluid. The two former provide the elastic elements and constraint for the fluid; and the latter, the viscous elements. The mechanical equivalent incorporating these elements is a system of dashpots (the lamellar surfaces and the interlamellar fluid) and springs (the lamellae and their interconnexions); it is a mechanical filter which suppresses low frequencies. The dynamic and static patterns of lamella displacements in the equivalent are in close agreement with those observed in Pacinian corpuscles.

3. Steady-state and transient pressure fields were determined for the equivalent. Under static compression, only elastic forces exist in the corpuscle. Analysis shows that such forces are transmitted poorly from periphery to centre through the lamellated structure. The compliance of the lamellar interconnexions is so high in relation to that of the lamellae themselves, that most of the pressure load is carried by the outer lamellae. As a result, only a small fraction of the steady-state pressure at the outer surface reaches the centre of the corpuscle where the sensory ending is located. This is the mechanical basis of receptor adaptation.

4. Under dynamic compression, viscous forces develop in the corpuscle; and these account for most of the pressure at times too early for development of elastic deformations. Analysis shows that such forces are transmitted well. For example, if a typical corpuscle of 500μ diameter is compressed by 20μ linearly during 2 msec, the pressure differences near to

the centre of the corpuscle are initially as high as at the periphery, and stay within the same order throughout the process of compression. In general, pressure at the centre increases steeply with velocity of compression. This explains the marked velocity dependence of the generator response of the sensory ending.

If, in the foregoing example, the 20μ compression is held fixed after 2 msec, the pressure differences at the centre fall abruptly to near zero with the onset of the static phase. The duration of pressure transients at the centre approximates that of the 'active' phase of the generator current of the sensory ending derived from experiments, as expected in a causal relationship: pressure difference \rightarrow generator current. Taken together with the earlier experimental finding of marked prolongation of generator response in corpuscles partially stripped of lamellae (Loewenstein & Mendelson, 1965), this result warrants the conclusion that the mechanical filter action of the corpuscle is the rate-limiting factor in generator response adaptation.

5. When the corpuscle is released from compression, energy stored in the elastic elements during compression is released and consumed in viscous flow. Thus, viscous pressure is produced anew. The magnitude of this pressure depends on the velocity of release. The pressure distribution is rotated by 90° with respect to that in compression; i.e. during release, compression occurs once again, but this time at right angles to the direction of initial compression. Experiments show that the sensory ending does not discriminate such a rotation; the polarity and order of magnitude of the generator response to compression in one plane are the same as in another. Analysis shows that considerable pressure differences may be developed at the centre of the corpuscle during releases at physiological velocities. For instance, in a passive return from a compression of 20μ , the pressure difference at the centre (and the generator current) is of the same order of magnitude as that in a compression of the velocity in 4. This accounts for the 'off'-response of the sensory ending in purely mechanical terms.

INTRODUCTION

The characteristics of the electrical response of the Pacinian corpuscle to mechanical stimulation, the generator potential, have been extensively studied under a variety of test procedures and conditions (Álvarez-Buylla & de Arellano, 1953; Gray & Sato, 1953; Loewenstein & Rathkamp, 1958; Diamond, Gray & Inman, 1958; Loewenstein, 1958, 1959, 1961*a*, *b*; Álvarez-Buylla & Remolina, 1959; Ishiko & Loewenstein, 1961; Inman & Peruzzi, 1961; Illyinsky, 1962; Loewenstein & Mendelson, 1965). The structure of the corpuscle is also well known (for recent studies, see

Pease & Quilliam, 1957; Cauna & Mannan, 1958; Shanthaveerappa & Bourne, 1963). However, the manner in which structure influences response is less well understood. The electrical response arises at the non-myelinated nerve ending, which is the transducer proper (Loewenstein & Rathkamp, 1958), and the mechanical energy that drives the transducer is transmitted through a fluid-filled lamellated capsule which serves as coupling between the external mechanical stimulus and the transducer. Clearly, the structure of this capsule must play an important role in determining the mechanical forces acting on the transducer and, hence, in determining the response characteristics of the transducer. The present article concerns this role. It develops an analysis of a mechanical model of the corpuscle which closely resembles the actual structure, and provides a theory which accounts for many features of the transducer response.

The structural features of the Pacinian corpuscle essential for the purposes of the present study are shown diagrammatically in Fig. 1. The sensitive nerve ending extends centrally for most of the length of the corpuscle. It is surrounded by a cylindrical core structure which consists of a closely packed laminated arrangement of membranes (lamellae). The core is in turn surrounded by a series of lamellae whose spacings increase with diameter and whose shapes range from nearly cylindrical close to the core, to rather spherical at the surface. The spaces between the lamellae are filled with a liquid which will be assumed to have mechanical properties of density and viscosity close to those of water.

The present study is concerned with the transmission of mechanical stimuli from the outer surface of the corpuscle through the lamellar structure to the surface of the core. There is another chain of events in the propagation of stimuli through the core itself and, finally, in the generation of the electrical output of the nerve ending under the mechanical stimulus it receives. This latter sequence is not considered here. The core structure is treated as a comparatively rigid element. The work of Hubbard (1958) makes it clear that the deflexions of the core are disproportionately small compared to those of the outer lamellae; the slope of the deflexion-radius curve is much less near the core than near the outer lamellae. Thus, as a first approximation, the core will be assumed to be rigid.

The analysis rests on the following mechanical notions: (i) A closed membrane lamella, such as a sphere or a spheroid filled with an incompressible fluid, tends to retain its shape by virtue of the elasticity of the lamella. After a deformation by an external force, it returns to its original shape by elastic force. (ii) In addition to elastic force, there is viscous force produced by deformation in a multi-layered lamella system (corpuscle) due to flow of fluid in the spaces between the lamellae. When the corpuscle is compressed, the spacing of the lamellae decreases along the

line of compression and increases at right angles to it. The lamellae are considered to be impermeable, so that fluid must flow between them. (iii) The lamellae are interconnected by elastic elements: a static displacement of one lamellae results in displacement of lamellae located some distance away. Such a propagation of displacement cannot be provided by fluid pressure under static conditions (see below).

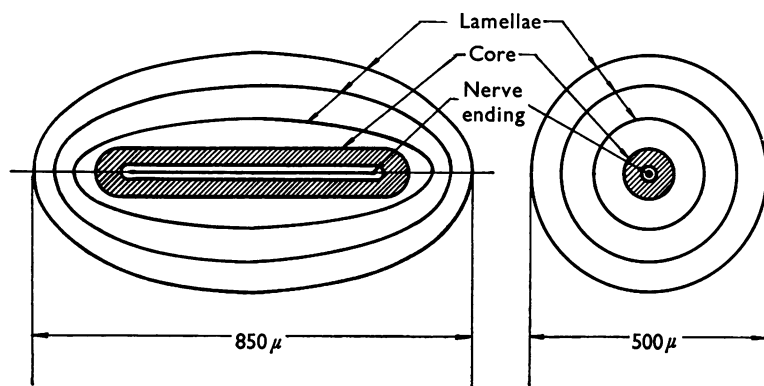


Fig. 1. Diagram of a Pacinian corpuscle in longitudinal and transverse sections showing principal elements of its structure. Dimensions are typical for a corpuscle of the cat mesentery.

Two models were considered in developing the analysis. First, a spherical model was used to study some properties and characteristics of a closed membrane system. The qualitative behaviour of the spherical model is discussed below. The spherical model represents the outermost lamellae of the Pacinian corpuscle quite well. However, the inner lamellae are more cylindrical in shape. To represent the entire corpuscle, a series of concentric cylindrical membranes was used as a second model. Displacement and pressure in response to static and dynamic stimulation were analysed for this model.

SPHERICAL MODEL

The mechanical notions above are valid for any closed membrane system. They are discussed below in terms of a spherical system. Each of the points made below has also been formulated analytically. The corresponding formulae have been derived, but are not included, since only the conceptual aspects of the spherical model will be used here.

The first idea is that an elastic membrane filled with a liquid tends to retain its shape. In the case of a sphere, if a compression is enforced along a certain diameter, the cross-section perpendicular to that diameter will increase, since the volume must remain constant. The stretching of the

perimeter of this cross-section results in a tension in the membrane which tends to restore the initial shape. This restoring force is one of the two principal elastic forces in the model of the Pacinian corpuscle.

Secondly, consider a rigid sphere surrounded by a slightly larger concentric spherical membrane with the space between the rigid sphere and the membrane filled with an incompressible fluid. If the spherical membrane is compressed along a diameter, it will again stretch along the equatorial plane. The fluid must flow away from the poles toward the equator during the compression, since the total volume remains constant. If the compression is applied slowly, fluid flow takes place easily; but, if the compression is applied rapidly, the flow may be appreciably hindered by the action of fluid viscosity. The flow through the narrow space between the rigid sphere and the membrane may require a substantial driving pressure at the poles. The pressure will be exerted on the rigid sphere, as well as on the fluid. This is one mechanism by which viscosity is assumed to promote transmission of pressure from lamella to lamella in the Pacinian corpuscle.

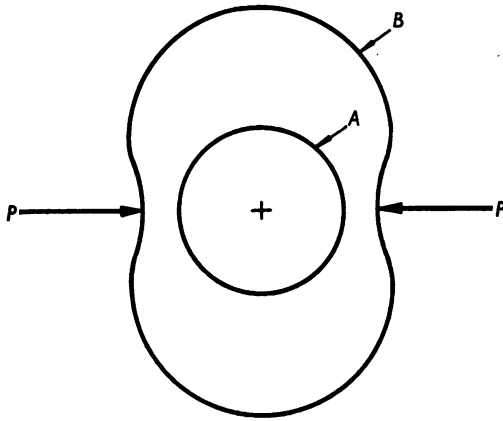


Fig. 2. Lamellated model. An inflated balloon, *A* is suspended inside another inflated balloon, *B*. *B* may be compressed by the forces *P* without distorting *A*.

The third notion of interest is that there must be elastic connexion between lamellae in the Pacinian corpuscle. A simple experiment with two balloons, as illustrated in Fig. 2, is instructive in this regard. A balloon, *A*, filled with a liquid, is suspended inside another balloon, *B*, similarly filled. If the balloon *B* is slowly compressed, the balloon *A* will not be deflected or distorted in any way, until the outer balloon, *B*, touches the inner one, *A*. In the Pacinian corpuscle, however, a static compression of the outermost lamella is transmitted to lamellae considerably below the surface (Hubbard, 1958). Hence, there must be more than fluid contact

between lamellae. In the model, weak elastic elements are assumed to connect adjacent lamellae in the radial dimension. These connexions are assumed to be uniformly distributed over the surface, and to be so thin as to offer no significant resistance to fluid flow between lamellae. The connexions presumably represent the occasional attachments between adjacent lamellae seen in photomicrographs (cf. Pease & Quilliam, 1957). The lamellae themselves are assumed to be impermeable for the brief periods considered in the mechanical analysis; fluid may flow between them, but not across them.

The above discussion rests, in part, on two ideas which are also of interest in themselves. The first is that in a fluid at rest, neglecting the effect of gravity, the pressure is uniform. Hence, the pressure in the space between two membranes is hydrostatic when the membranes are at rest. Secondly, a uniform pressure applied to a membrane filled with an incompressible fluid produces no deformation. The only result is to raise the pressure throughout the enclosed fluid by the amount of the applied pressure. Hence, in dealing with pressures applied to the Pacinian corpuscle, only the non-uniform part of the pressure distribution will be assumed to produce deformation; the uniform component or hydrostatic pressure will be disregarded. This assumes, in turn, that the transducer element of the nerve ending of the Pacinian corpuscle is sensitive to distortional strain and not to hydrostatic stress. There is no direct evidence for this in the Pacinian corpuscle. It is difficult to obtain such evidence, because of the very fast adaptation of the corpuscle's electrical response; and attempts in this direction have failed for technical reasons (Goldman, D., and Gray, J. A. B., personal communication). However, definite information on this point is available in a more slowly adapting mechano-sensitive nerve ending, in which this difficulty does not exist, and in which it is clear that distortional strain but not hydrostatic stress elicits electrical responses (Loewenstein, 1960).

The ideas discussed above are presented in terms of a spherical geometry, because this case is readily visualized. In the subsequent analysis, a cylindrical model is used, which is more realistic for the inner lamellae of the corpuscle. However, the assumptions of the analysis are such that all of the ideas and conclusions drawn above remain valid and are retained.

CYLINDRICAL MODEL

The cylindrical model is shown schematically in Fig. 3. The core of the corpuscle is represented by a solid circular cylinder which, for the purposes of the present analysis, is considered to be rigid. At each end of the core, there are rigid circular terminal plates to which the various lamellae are attached.

The spaces between the lamellae are filled with an incompressible viscous fluid. The lamellae are sealed against fluid leakage at the terminal plates so that the volume enclosed by any lamella is fixed during deformation of the corpuscle. With respect to stresses developed in the lamellae, the ends supported by the terminal plates are simply supported, i.e. free to move in the direction parallel to the axis of the cylinder.

Adjacent lamellae are connected by radial connexions which hold the lamellae in position at rest. These connexions play the same role as in the spherical model; they are weak, thin springs which are distributed uniformly and do not restrict fluid flow.

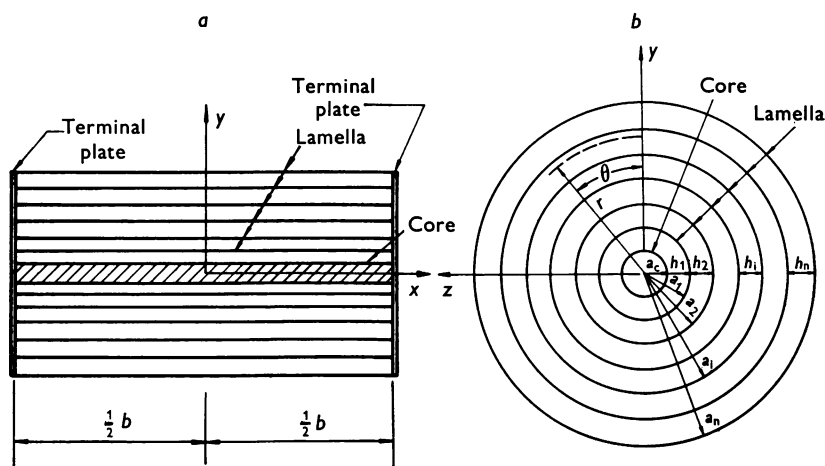


Fig. 3. Cylindrical model of a Pacinian corpuscle. (a) Longitudinal cross-section. (b) Transverse cross-section. Explanation in the text.

A squeezing action on the cylindrical model may be produced by a pressure distribution on the surface of the corpuscle which is symmetric with respect to the plane $\theta = \pm \frac{1}{2}\pi$ (Fig. 3b). It is assumed that the pressure distribution is symmetric with respect to the plane $x = 0$ (Fig. 3a). Any such distribution may be represented by a double Fourier series of the form

$$p = p_0 + \sum_k \sum_m A_{km} \cos(2k\theta) \cos\left(m\pi \frac{x}{b}\right), \quad (1)$$

where k and m each take on the values 1, 2, 3, ..., and the amplitude coefficients A_{km} have the units of pressure, dyn/cm². The term p_0 represents a uniform hydrostatic pressure equal to the mean of p . The remaining terms of the series each have a zero mean. The hydrostatic term p_0 raises the pressure by p_0 throughout the model, but produces no deflexion and is assumed also to have no effect on the nerve ending of the corpuscle.

The restriction to symmetric pressure distribution with respect to x may be removed by including a second series of the form $\Sigma \Sigma A'_{km} \cos(2k\theta) (\sin m\pi x/b)$ in eqn. (1). The analysis for such pressure distribution is similar to that given below for the symmetric distribution represented by the A_{km} terms in eqn. (1).

Each of the A_{km} terms will produce a deformation of the corpuscle proportional to $\cos(2k\theta) \cos(m\pi x/b)$. However, it may be expected that the elastic resistance of any lamella will increase with both k and m , but the viscous resistance will decrease as k and m increase. Since the time constant in any mode is proportional to the ratio of viscous resistance to elastic modulus, it follows that the lowest frequency response will be achieved by the lowest mode, i.e. $k = m = 1$. Hence this mode is singled out and treated exclusively in the remainder of the analysis. Henceforth the term 'pressure' will be used to designate the symmetric component whose amplitude coefficient is A_{11} in eqn. (1).

Consider the i th membrane, Fig. 3, under the pressure p_i given by

$$p_i = A_i \cos(2\theta) \cos\left(\pi \frac{x}{b}\right), \quad (2)$$

where A_i is a coefficient equal to the maximum value of the pressure p_i , dyn/cm². In the absence of the radial springs connecting the lamellae, the deflexion w_i of the membrane at any point will be

$$w_i = B_i \cos(2\theta) \cos\left(\pi \frac{x}{b}\right), \quad (3)$$

where w_i = radial deflexion measured positive inward (cm),

$$B_i = A_i K_i, \quad K_i = \frac{a_i^2}{E d_i} \left(1 + \frac{4b^2}{\pi^2 a_i^2}\right)^2, \quad (4)$$

K_i = compliance of the i th membrane (cm³/dyn),

a_i = radius of the i th lamella (cm),

d_i = thickness of the i th lamella (cm),

b = length of the corpuscle (cm),

E = Young's modulus (dyn/cm²).

Eqns. (3) and (4) are derived in Appendix A.

Consider next the stress developed in the radial springs in the i th fluid-filled space. This stress, σ_i , will depend on the relative motion of the i th and $(i-1)$ th lamellae (Fig. 3b). The stress will be the product of the

strain and the elastic modulus which is assumed to be αE , where α is a constant much less than unity, since the springs are thin and soft. Thus

$$\sigma_i = \frac{w_i - w_{i-1}}{h_i} \alpha E, \quad (5)$$

where h_i = spacing of the i th lamella (cm) (Fig. 3b), and the remaining symbols are the same as used previously. Assuming both w_i and w_{i-1} to contain the factor $\cos(2\theta) \cos(\pi x/b)$, eqn. (5) may be written

$$\sigma_i = C_i \cos(2\theta) \cos\left(\pi \frac{x}{b}\right). \quad (6)$$

Combining eqns. (3), (5) and (6) yields

$$C_i = \frac{B_i - B_{i-1}}{h_i} \alpha E. \quad (7)$$

Finally, consider the fluid motion in the i th fluid-filled space. Under a relative velocity $(\dot{w}_i - \dot{w}_{i-1})$, where the dots denote differentiation with respect to time, there will be a viscous pressure \bar{p}_i generated in the fluid of the form

$$\bar{p}_i = D_i \cos(2\theta) \cos\left(\pi \frac{x}{b}\right), \quad (8)$$

where D_i is an amplitude coefficient, dyn/cm². It is shown in Appendix B that D_i is given by

$$D_i = R_i (\dot{B}_i - \dot{B}_{i-1}), \quad (9)$$

where

$$R_i = \frac{12\mu b^3}{h_i^3 \pi^2 \left(1 + \frac{4b^2}{\pi^2 a_i^2}\right)}, \quad (10)$$

where b , a_i and h_i are used as previously defined; R_i is a viscous resistance coefficient, dyn sec/cm³; and μ is the fluid viscosity, dyn sec/cm².

In the derivation of eqn. (10) the inertia of the fluid is neglected, because the Reynolds number of the flow is small. In considering the motion of each lamella, the inertia of the lamella is also neglected. Then the equation of motion of any lamella reduces to the statement that the deflexion of the lamella at any time is the static deflexion that would be produced by the instantaneous load, if it were held constant. This load is the difference of the viscous fluid pressure and the radial spring stress on each side of the lamella. For the i th lamella the equation is

$$p_i = \frac{w_i}{K_i} = \bar{p}_{i+1} + \sigma_{i+1} - \bar{p}_i - \sigma_i, \quad (11)$$

or in terms of the various coefficients

$$\frac{B_i}{K_i} = R_{i+1}(\dot{B}_{i+1} - \dot{B}_i) + \frac{B_{i+1} - B_i}{h_{i+1}} \alpha E - R_i(\dot{B}_i - \dot{B}_{i-1}) - \frac{B_i - B_{i-1}}{h_i} \alpha E. \quad (12)$$

The eqn. (12) applies to every lamella, except the first and the last. For the outermost (n th) lamella, the first two terms on the right in eqn. (12) are replaced by A_n , the coefficient of the external pressure applied to the n th membrane. For the first membrane adjacent to the core, \dot{B}_{i-1} and B_{i-1} in eqn. (12) are set equal to zero to represent the stationary core.

MECHANICAL AND ELECTRICAL ANALOGUES

One may now discuss and to some extent compute solutions of the system of equations represented by eqn. (12) in terms of an electrical analogue. This allows one to use standard electrical network theory in the computations; and is also helpful in clarifying some of the concepts involved which may be more readily understood, perhaps, in an electrical analogue than in a mechanical one.

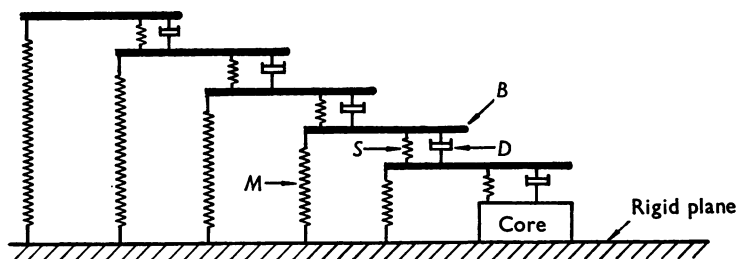


Fig. 4. Mechanical analogue of the Pacinian corpuscle. Lamella compliance is represented by springs M ; radial spring compliance, by springs S ; and the fluid resistance, by dashpots D .

Mechanical analogue. In constructing analogues it is convenient to consider only half of the corpuscle at a time. If a horizontal plane is passed through mid-height of Fig. 3b, the two halves are mirror images, and the displacements and pressure are also symmetrical with respect to this plane. The action of any lamella may be regarded as transferring a load from the lamella to this plane. The pressure due to viscous action of the fluid is equivalent to a dashpot connecting adjacent lamellae. The radial lamella connexions act in parallel with this dashpot. The mechanical analogue is shown schematically in Fig. 4. The horizontal bars (B) represent lamellae. These bars are rigid and weightless in the analogue, and are constrained to move vertically only, remaining parallel to their original

position. The compliance of the springs (M) connecting the bars to the rigid plane corresponds to the lamella compliance K_i . The springs (S) paralleling the dashpots are the radial lamella connexions and have the compliance $h_i/\alpha E$. The dashpots (D) have the viscous resistance R_i . If the displacement of the i th bar in the mechanical analogue, measured positive downwards, be denoted B_i , then it may be verified that eqn. (12) holds for the analogue by considering the motion of each bar.

Figure 4 displays half of the core which is subject to the forces transmitted by the first radial spring and the first dashpot, corresponding to the stresses transmitted through the first fluid layer in the corpuscle.

TABLE 1

Mechanical quantity	Electrical quantity
Pressure, p , dyn/cm ²	Voltage, E , volts
Displacement, w , cm	Charge, Q , coulombs
Velocity, \dot{w} , cm/sec	Current, I , amperes
Mass, M , g	Inductance, L , henries
Viscous resistance, R , dyn sec/cm ²	Resistance, R , ohms
Compliance, K , cm ² /dyn	Capacitance, C_m , farads
Compliance, $h/\alpha E$, cm ² /dyn	Capacitance, C_s , farads

Electrical analogue. The mechanical analogue may now be translated into an electrical one using the usual correspondences (cf. Mason, 1942). Table 1 summarizes the mechanical quantities used for the Pacinian corpuscle. In the mechanical analogue, pressure is replaced by force, and the units of resistance and compliance are dyn sec/cm and cm/dyn. Mass and inertial effects have been neglected in the present theory; the electric analogue contains, therefore, no inductance.

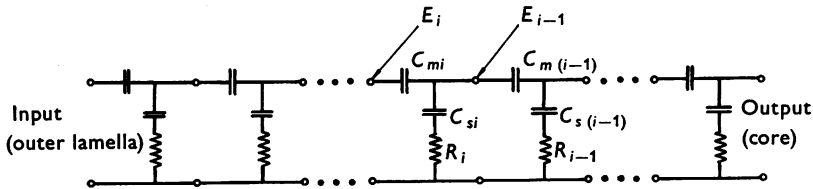


Fig. 5. Electrical analogue of the capsule of a Pacinian corpuscle in which the lamella compliance, K_i , is represented by the capacitance C_{mi} ; the radial spring compliance, $h_i/\alpha E$, by the capacitance C_{si} ; and the fluid resistance (R_i), by the electrical resistance, R_i .

The electrical analogue is illustrated in Fig. 5. Each segment of the ladder network corresponds to one lamella and its associated fluid space. Thirty such lamellar units, five of which appear in Figs. 4 and 5, are taken into account in the computations. Note that the parallel spring and dashpot transform into a series combination of capacitance and resistance.

The validity of the electric analogue is established by writing the

equations governing the network. The voltage across the right-hand terminals of the i th segment (Fig. 5) is E_{i-1} given by

$$E_{i-1} = \frac{Q_{si}}{C_{si}} + R_i \dot{Q}_{si}. \quad (13)$$

The voltage across C_{mi} is

$$E_i - E_{i-1} = \frac{Q_{mi}}{C_{mi}}. \quad (14)$$

Kirchoff's law may be written in the form

$$Q_{mi} - Q_{m(i-1)} = Q_{si}, \quad (15)$$

where Q_{mi} and Q_{si} are the charges on C_{mi} and C_{si} , respectively. Substituting eqn. (15) into eqn. (13)

$$E_{i-1} = \frac{Q_{mi}}{C_{si}} - \frac{Q_{m(i-1)}}{C_{si}} + R_i \dot{Q}_{mi} - R_i \dot{Q}_{m(i-1)}. \quad (16)$$

A similar equation may be written for E_i ; if this equation for E_i and eqn. (16) for E_{i-1} are substituted in eqn. (14), the result may be written in the form

$$\frac{Q_{mi}}{C_{mi}} = \frac{1}{C_{s(i+1)}} (Q_{m(i+1)} - Q_{mi}) - \frac{1}{C_{si}} (Q_{mi} - Q_{m(i-1)}) + R_{i+1} (\dot{Q}_{m(i+1)} - \dot{Q}_{mi}) - R_i (\dot{Q}_{mi} - \dot{Q}_{m(i-1)}). \quad (17)$$

This, (17), is the electrical equivalent of eqn. (12).

The voltage E_i represents the total pressure applied to the i th lamella. The voltage drop across C_{mi} represents the portion of the applied pressure carried by the i th lamella. The voltage drops across C_{si} and R_i are the analogues of the pressures σ_i and \bar{p}_i transmitted by the radial springs and viscous fluid action through the i th fluid layer.

In the following, the results of the computations of lamella displacement will be given first, to be compared with available experimental displacement data. Then the results of the computations of pressure, particularly of core pressure, will be given. These will be compared with their transduced effects, the generator currents.

NUMERICAL EXAMPLES

Computations were carried out for the cylindrical model of Fig. 3 with the over-all dimensions given in Table 2.

TABLE 2. Cylindrical model dimensions

Over-all length, b	700 μ
Core radius, a_c	20 μ
Outer lamella radius, a_n	255 μ
Number of lamellae, n	30
Thickness of lamellae, d_i	1 μ

The lamella spacing is such that the radii of successive lamella, a_i , and a_{i+1} , are related by

$$a_{i+1} = \gamma a_i, \quad (18)$$

where $\gamma = 1.083$ for the first twenty lamellae and 1.10 for the last ten. This spacing is typical of the Pacinian corpuscle (Hubbard, 1958). The thickness of a lamella in the Pacinian corpuscles is about 1μ (Pease & Quilliam, 1957). The fluid layer thickness between lamellae was thus taken as the difference of adjacent lamella radii minus 1μ .

TABLE 3. Dimensions and constants of the model of the Pacinian corpuscle

Lamella no.	Radius (μ)	Lamella compliance* $K_t(\text{cm}^3/\text{dyn})$	Radial springs' compliance, $h_i/\alpha E^*$ (cm^3/dyn)	Viscous resistance,* $R_t(\text{dyn sec}/\text{cm}^3)$
Core	20.0	—	—	—
1	21.7	1.69×10^{-3}	1.32×10^{-7}	4.88×10^5
2	23.5	1.44×10^{-3}	1.59×10^{-7}	3.24×10^5
3	25.4	1.23×10^{-3}	1.89×10^{-7}	2.27×10^5
4	27.5	1.05×10^{-3}	2.22×10^{-7}	1.66×10^5
5	29.8	8.96×10^{-4}	2.57×10^{-7}	1.25×10^5
6	32.3	7.65×10^{-4}	2.95×10^{-7}	9.72×10^4
7	34.9	6.54×10^{-4}	3.36×10^{-7}	7.70×10^4
8	37.8	5.58×10^{-4}	3.80×10^{-7}	6.21×10^4
9	41.0	4.77×10^{-4}	4.28×10^{-7}	5.09×10^4
10	44.4	4.08×10^{-4}	4.80×10^{-7}	4.22×10^4
11	48.1	3.49×10^{-4}	5.37×10^{-7}	3.54×10^4
12	52.1	2.99×10^{-4}	5.98×10^{-7}	3.00×10^4
13	56.4	2.56×10^{-4}	6.64×10^{-7}	2.56×10^4
14	61.1	2.19×10^{-4}	7.36×10^{-7}	2.20×10^4
15	66.1	1.88×10^{-4}	8.14×10^{-7}	1.91×10^4
16	71.6	1.62×10^{-4}	8.98×10^{-7}	1.66×10^4
17	77.6	1.39×10^{-4}	9.89×10^{-7}	1.45×10^4
18	84.0	1.20×10^{-4}	1.09×10^{-6}	1.27×10^4
19	91.0	1.03×10^{-4}	1.19×10^{-6}	1.12×10^4
20	98.5	8.94×10^{-5}	1.31×10^{-6}	9.87×10^3
21	108.4	7.53×10^{-5}	1.77×10^{-6}	4.79×10^3
22	119.2	6.37×10^{-5}	1.97×10^{-6}	4.18×10^3
23	131.2	5.41×10^{-5}	2.18×10^{-6}	3.64×10^3
24	144.3	4.62×10^{-5}	2.42×10^{-6}	3.18×10^3
25	158.7	3.98×10^{-5}	2.68×10^{-6}	2.77×10^3
26	174.6	3.44×10^{-5}	2.97×10^{-6}	2.41×10^3
27	192.0	3.01×10^{-5}	3.29×10^{-6}	2.09×10^3
28	211.2	2.65×10^{-5}	3.64×10^{-6}	1.81×10^3
29	232.3	2.36×10^{-5}	4.02×10^{-6}	1.56×10^3
30	255.6	2.13×10^{-5}	4.45×10^{-6}	1.34×10^3

* For electrical equivalents see Table 1.

The density and viscosity of the fluid were taken to be the same as of water, i.e. $1 \text{ g}/\text{cm}^3$ and $0.01 \text{ dyn sec}/\text{cm}^2$, respectively. The modulus of elasticity, E , was assumed to be $5 \times 10^6 \text{ dyn}/\text{cm}^2$. This value is typical of tissues such as arterial walls (McDonald, 1960) and we assumed that it is of the same order for the corpuscle. The coefficient α which controls the compliance of the radial springs was determined by making a number of computational runs with various values for α and selecting the value

which had the best fit with Hubbard's (1958) displacement data for the Pacinian corpuscle. The coefficient used was $\alpha = 0.0001$.

Three types of computations were carried out: (a) For a static displacement applied to the corpuscle, an analysis of the electrical analogue was performed with a fixed input voltage, neglecting the presence of the resistances. (b) For various fixed frequencies of input voltage, the steady-state response of the electrical analogue was computed using standard network theory. (c) The transient response of the system was determined by integrating the set of differential equations (12) numerically by a finite difference technique. All computations were performed on an IBM 7094 computer.

As to the first step, the dimensions, compliances and resistances were computed from the data in Table 2 and eqns. (18), (4), (5) and (10). Table 3 gives the results. Once these coefficients were determined, electrical network theory was employed in setting up the computations of displacements and pressures, using the translation given in Table 1.

COMPRESSION

Displacements

Static displacements. The term static displacement is used here to denote the change in radius of any lamella from its normal position, when the corpuscle is subjected to a compression which is held fixed for a long time or is applied at a very slow rate. In this static state, there are no velocities in the corpuscle and, hence, in the electric analogues there are no currents. The resistances in the circuit then play no role. The application of a static pressure to the corpuscle corresponds to applying a fixed voltage to the analogue network which then acts as capacitive voltage divider. All we need to solve this case is the relation between charge and voltage on a capacitor, plus the notion that the charge must be conserved by Kirchhoff's law (eqn. 15).

The static displacements computed for various amounts of total compression of the corpuscle are shown in Fig. 6. To be precise, the ordinates are the coefficients B_i in eqn. (3); each value is equal to the maximum displacement of any point on a given lamella. The abscissa is the radius measured from the axis of the corpuscle. The numbers on the curves give the total compression applied, which equals twice the displacement of the outermost lamella. The displacement, at any radius, is proportional to the applied compression in the present linear theory.

The theoretical curves in Fig. 6 are in good qualitative agreement with the experimental measurements of lamella displacements reported by Hubbard (1958). The static displacement decreases rapidly with radius,

and becomes nearly zero in the range of radii close to the core. In this range, the displacements are too small to be measured with Hubbard's techniques, which may account for their being reported as zero (Hubbard,

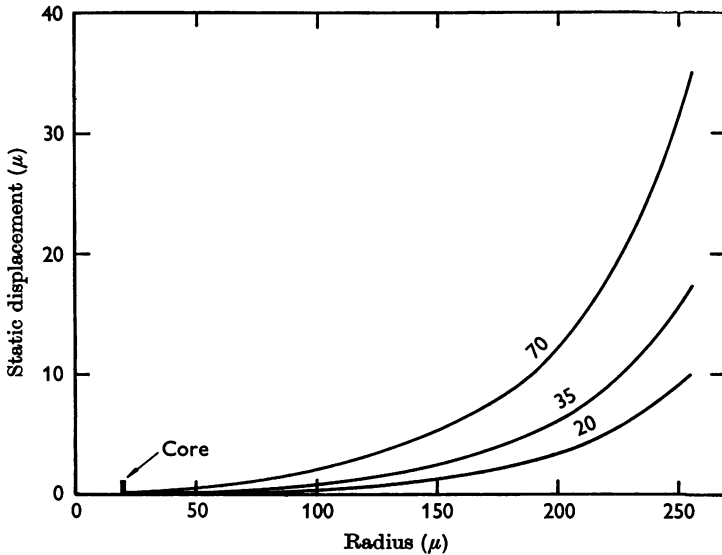


Fig. 6. Computed static lamella displacement. The numbers on the curves are the total compressions in μ applied to the outermost lamella.

1958). In both the theoretical treatment here and Hubbard's experimental results, the displacement is proportional to the applied compression.

A feature of Hubbard's experiments which is not reproduced by the present theoretical treatment is a levelling off of the displacement-radius curves near the outermost lamellae (Hubbard, 1958, Fig. 11). This is probably due to the fact that in Hubbard's experiments the compression is large, and the displacement is measured perpendicular to the applied compression. These factors introduce non-linearity at large compressions.

Dynamic displacement. A mode of stimulation of particular physiological interest is that of a suddenly applied pulse of displacement or velocity. We will consider here the case of a total compression of 20μ accomplished with a uniform velocity in 2 msec. This case was selected for computation, because it is within the ranges of displacement and velocity of physiological stimuli, and because it is the type of stimulus often used in experimental work with Pacinian corpuscles for which much information on its electrical response is available.

The corresponding problem in the electric analogue is that of finding the currents, voltages, and charges in the network for a constant current input during the 2 msec of imposed velocity and zero current input upon ces-

sation of the outer lamella movement. This problem was solved numerically by considering a series of small time steps ($\Delta t = 0.1$ msec) during each of which the currents flowing in the circuit were assumed to be constant. The charge on each capacitor is equal to the integral of the current flowing through it, and its voltage is adjusted accordingly at the end of each time interval. Based on these new voltages, the currents flowing were re-computed, assumed constant for the next time interval, and so on. The initial charges and voltages on all capacitors are zero and the initial voltages across each of the resistances in the analogue circuit are equal. The magnitude of this voltage is the product of the input current and the effective resistance of all 30 parallel resistors R_i .

Results of the transient computations are shown in Fig. 7. The total displacements of three different lamellae are given as functions of time in Fig. 7*a*. To make a full comparison with Hubbard's experimental data, we have computed also the 'equivalent static' and 'dynamic' displacements, as used by Hubbard. Figure 7*b* shows the 'equivalent static displacement', which is the displacement which would result if the instantaneous displacement of the outermost lamella were held fixed for a long time. Figure 7*c* shows the 'dynamic' component of displacement, which is the total displacement of Fig. 7*a*, minus the 'equivalent static displacement' of Fig. 7*b*.

The computed curves in Fig. 7 are in good qualitative agreement with the experimental observations reported by Hubbard (1958). Some points of agreement are as follows.

The total displacement increases steadily during the entire 2 msec course of applied compression. Thereafter, the displacements of the inner lamellae decrease with a time constant of the order of a few milliseconds. The asymptotic values of the total displacements are, of course, the respective static values.

Both the computed and experimental curves of static displacement have a ramp shape. The rounding at the peak of Hubbard's experimental curves, which is absent in the computed curve of Fig. 7*b*, is due to differences in stimulation. While for the computed results compression is ideally ramp-shaped, in Hubbard's experiments the applied compressions were rounded at their peaks.

The curves of dynamic displacement in Fig. 7*c* resemble those of Hubbard in shape and in order of decay time. Moreover, in both experimental and theoretical values all displacements decrease with radius over the range shown in Fig. 7. (By definition, the dynamic displacement is zero at the outermost lamella.) A point of apparent disagreement concerns the ratio of the peak dynamic to the static displacement close to the core. The ratio is larger in the experimental curves. This may possibly be due to the difficulty of resolving the small static displacements near the core

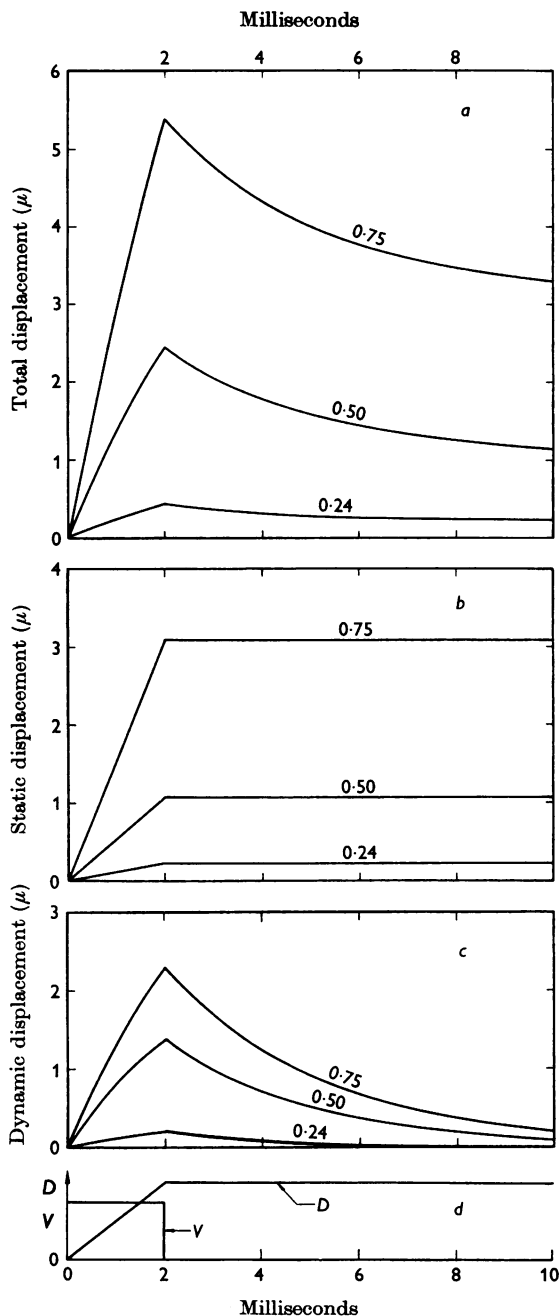


Fig. 7. Computed displacements of selected lamellae against time for a total compression of $20\ \mu$ applied uniformly in 2 msec and then maintained. The number identifying each curve is the ratio of the particular lamella radius, for which the displacement is shown, to the radius of the outermost lamella. Outer boundary of core is at ratio 0.078. (a) Total displacement. (b) Equivalent static displacement. (c) Dynamic component of displacement (see text for definitions). (d) Displacement (D) and velocity (V) of outermost lamella.

in the experiments. For the peripheral lamellae, the ratios are in good agreement.

In general, the computed displacements, both static and dynamic, reproduce the features of the experimental values sufficiently well to give confidence that the concepts underlying the present model are valid.

Pressure

With this encouraging agreement between computed and experimental lamella displacements, we proceeded to compute the pressures inside the

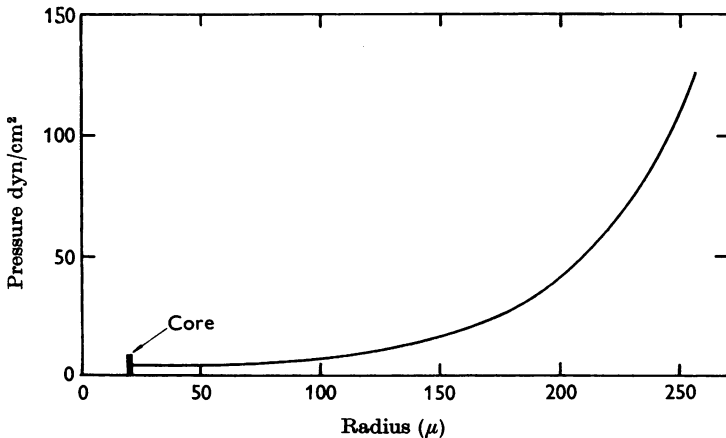


Fig. 8. Computed static pressure on lamellae against radius, for a static compression of 20μ applied to the outermost lamella.

corpuscle. The final effect of the mechanical transmission through the corpuscle is the pressure distribution exerted on the core. This is the factor which is directly responsible for the electrical transducer response. Lamella displacements outside the core are not of themselves of interest, except in that they participate in the transmission of this pressure. This is where the computations were able to go beyond the experimental work. The pressures which are at present not measurable inside the small corpuscle can be computed for the model and compared with the transducer response. These pressures exerted on any given lamella are the voltages E_i applied to the capacitances C_{mi} in the electrical analogue.

Static pressure. Figure 8 gives the pressures computed for the case of a static compression of 20μ . The striking feature of the pressure curve is that the static pressure on the core is only a small fraction (3 %) of that on the outermost lamella. This is chiefly due to the preponderance of the stiffness of the lamella (M , Fig. 4) over that of the radial lamellar connexions (S). Thus, the pressure load is picked up largely by the outer

lamellae, and very little pressure reaches the interior of the corpuscle. This constitutes the basis of the phenomenon of receptor response adaptation under static compression, discussed in detail further on.

Dynamic pressure. (a) Sinusoidal stimulation. The computation of the core pressure at any frequency may be treated as a problem in alternating current theory applied to the network of Fig. 5. The electrical equivalents of the mechanical quantities are given in Table 1. We utilized a computer program already written for a generalized ladder network which was kindly made available to us by Professor O. Wing and Mr S. Brueck, Department of Electrical Engineering, Columbia University. The program starts from any given output voltage (alternating pressure on the core), and proceeds to compute the impedances, currents and voltages at each of the subsequent junctions.

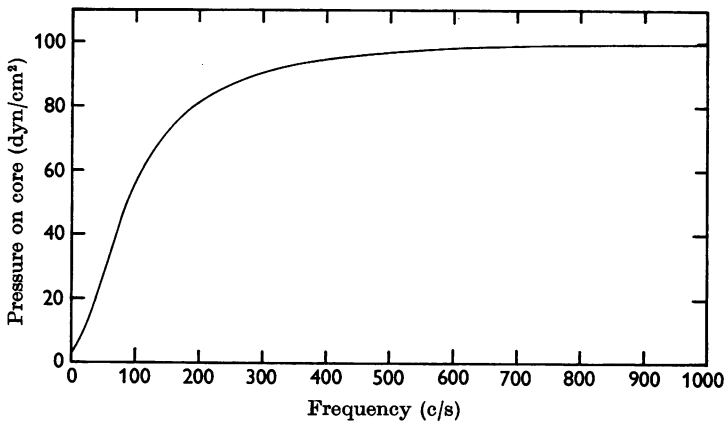


Fig. 9. Core pressure against sinusoidal stimulus frequency. Computed core pressure resulting from sinusoidal displacement of the outermost lamella at constant peak pressure of 100 dyn/cm².

The main result of the computation is shown in Fig. 9. The ordinate is the peak pressure exerted on the core for a peak pressure of 100 dyn/cm² on the outermost lamella at the frequencies given by the abscissa. Each pressure has the spatial distribution given by eqn. (2) and is sinusoidal in time. Zero frequency corresponds to the static case in which the pressure transmitted to the core is only 3% of the applied pressure. At high frequencies, *circa* 300 c/s, the pressure on the core is 90% or more of the applied pressure. Most of the pressure transmitted is due to the viscous action of the interlamellar fluid. In the electric analogue, this action corresponds to the predominance of the resistive elements over the capacitive impedance at high frequency.

(b) Linear stimulation. Computations of the dynamic pressure resulting from a ramp-compression were made on the basis of eqn. (12). Figure 10

shows the peak pressures on the outermost lamella, on the core and on one intermediate lamella resulting from a compression, as used above for the analysis of dynamic displacement (Fig. 7). The pressures have the spatial distribution given by eqn. (2) in each case.

At the moment the motion is initiated (time zero), the pressure, entirely of viscous origin, is uniform from the outermost lamella to the core. As the lamellae deflect and pick up the load, the pressure on the outermost lamella increases and the pressure on the core decreases. At the time the motion of the outermost lamella ceases (2 msec), there is a large and sudden drop in the pressure throughout the corpuscle. This is due to a corresponding change in the viscous component of force: the decrease in velocity of the outer lamella at time 2 msec produces a drop in fluid pressure throughout the corpuscle which is equal to the rise in pressure produced by the increase in velocity at time zero, since the system is linear. For the constants assumed for the present model, the pressure on the core goes slightly negative. A negative sign here means simply that the local force vector has reversed direction. This is associated with a rotation of the entire pressure distribution by 90° in θ with respect to the compressed case (eqn. (2); Fig. 3). But the main point is that at time 2 msec the core pressure drops to near zero. The core pressure roughly follows the applied velocity.

Some qualitative aspects of the results on pressure transmission (Fig. 10) are immediately clear from an inspection of the electrical analogue, which operates as a high-pass filter. The application of a step velocity to the corpuscle corresponds to applying a step current to the electrical analogue (Fig. 5). The resulting initial voltage will be immediately applied to every resistor in the network, and a set of currents will start to flow as if the capacitances, initially uncharged, were absent. (In mechanical terms, this means that all the pressure applied is immediately transmitted to the core by viscous action without loss, and fluid starts to flow between lamellae.) As time proceeds, the capacitive voltages increase and become relatively more important than the resistive ones. In the final static state, the current is zero and the network acts as a purely capacitive voltage divider: the voltage drops across each capacitance C_m from outside to core (Fig. 5). The increase in C_m (lamella compliance) and the decrease in C_s (lamellar connexion compliance) from outside to core, and the relative values of C_m and C_s , all concur in causing the voltage (pressure) drop to be steep (Fig. 8).

DE-COMPRESSION

When a Pacinian corpuscle is released suddenly from its compressed state, a second generator response (off-response) is produced which is similar to that produced during the dynamic phase of the compression

(on-response) (Gray & Sato, 1953). To clarify the origin of the off-response, we have computed the pressure transients inside the corpuscle during a

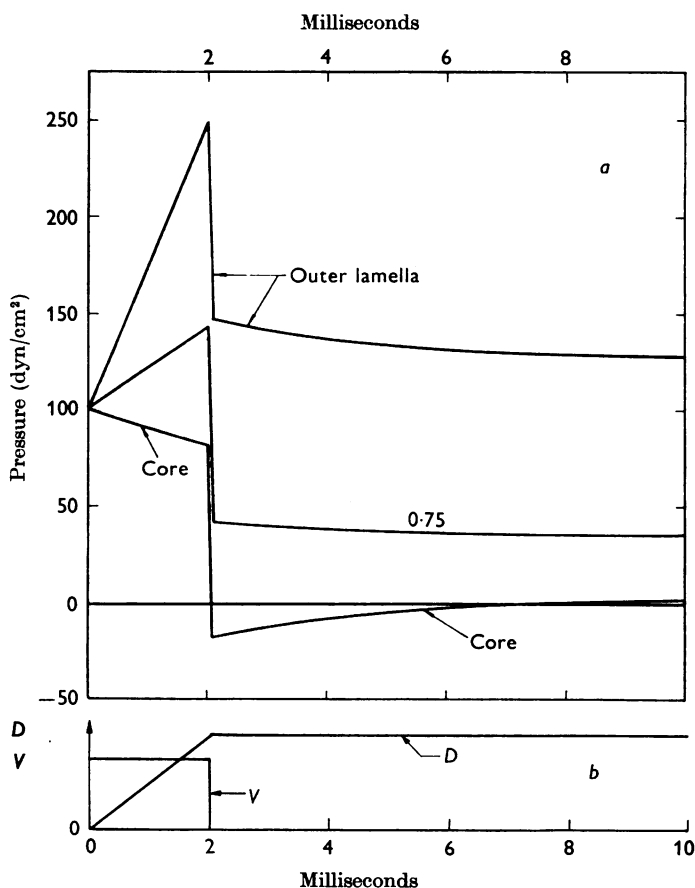


Fig. 10. Time course of dynamic pressure. (a) Computed pressure on outermost lamella, at 0.75 of corpuscle radius, and on the core against time for a total compression of 20μ applied uniformly in 2 msec and then maintained. (b) Displacement (D) and velocity (V) of outermost lamella.

sudden release from a static compression. During such a release, the corpuscle tends to return to its circular cross-section under the action of the elastic forces generated by the lamellae and their radial connexions. The action may be equated to applying a negative pressure to the outermost lamella so as to bring the net pressure on it to zero. The negative pressure here considered develops with sufficient velocity so that the rate-limiting factor of motion is that given by the passive elastic return of the lamellae. This clearly corresponds to the situation in which electrical

off-responses are elicited under physiological conditions (see, for example, inset of Fig. 14).

The resultant pressure on any lamella is computed as the static pressure responsible for the positive pressure during compression, plus the transient pressure response to the negative pressure parenthesis eqn. (12). Figure 11 gives the time course of the computed pressure on the core for a sudden release from a static compression of 20μ . The rate of release here is unrestrained by external mechanical forces and is solely determined by the

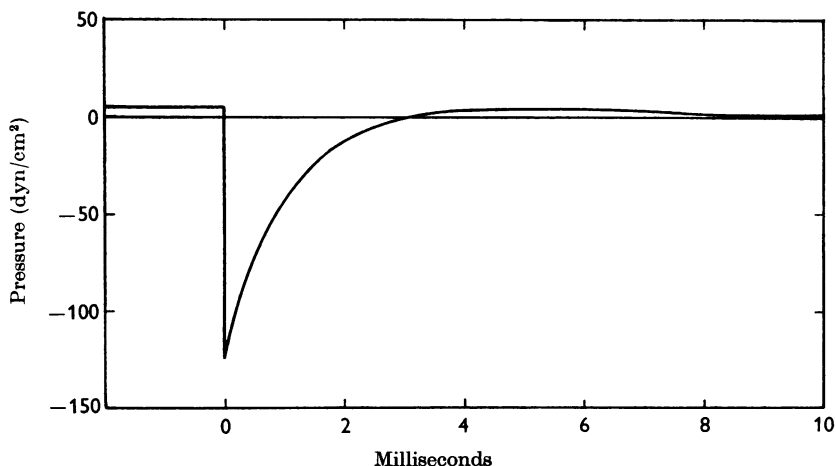


Fig. 11. Pressure during 'off'-phase. Pressure on core against time for a sudden release from a total compression of 20μ . Negative sign stands for reversal in direction of total pressure. See text.

mechanical constants of the lamella system. The core pressure, nearly zero in the static state, rises abruptly to about -122 dyn/cm^2 upon release of compression. At the moment of release, as in the initial phase of dynamic compression discussed before, the change in the pressure on the core is purely viscous and uniform throughout the corpuscle. Thereafter, the pressure on the core decays to zero in a few milliseconds, as the velocities in the system decrease.

PHYSIOLOGICAL CORRELATES

Receptor adaptation

The present analysis sheds light on the mechanisms of various physiological phenomena. We will consider first those concerning receptor adaptation. This wide-spread phenomenon in mechanoreceptors (particularly marked in receptors of the lamellated type) manifests itself, at the generator level, as a decrease in amplitude of electrical output with

decreasing stimulus velocity (cf. Gray & Sato, 1953; Álvarez-Buylla & Remolina, 1959).

Adaptation to static loading. Both the physical aspects and the physiological meaning of adaptation are well illustrated by experiments in which a Pacinian corpuscle is compressed to a fixed level and this level is maintained for some time. The resulting generator potential declines then to zero within a few milliseconds, regardless of the duration of the compression (see, for example, Fig. 12).

The steady phase of the stimulation corresponds clearly to the conditions of static loading analysed before (Fig. 8). As the analysis shows, there is little pressure in this condition at the centre of the corpuscle where the transducer nerve ending is located. Under static compression, pressure in the capsule is only of elastic origin, and such pressure propagates poorly from periphery to centre, because the compliance of the radial lamella connexions is high relative to that of the lamellae themselves. The pressure exerted on the outermost lamella, in part, is carried by the lamella itself (M ; Fig. 4), and, in part, passed on to the next lamella by the radial lamella connexions (S); and so on. The connexions are so compliant, however, that almost the entire pressure load is picked up by the outer lamellae; the pressure finally passed on to the core has dropped two orders of magnitude (Fig. 8).

During the initial dynamic phase of the compression, the situation is quite different. Until the compression reaches its static level, the existing fluid velocities set up pressures by viscous action, and such pressures propagate well from periphery to centre. In a ramp-shaped compression, the pressure on the core is of the same order as that on the periphery of the capsule, before the static level is attained (Fig. 10). At the onset of compression, the core pressure is, in fact, equal to the peripheral one. During the remainder of the dynamic phase, the pressure on the core becomes relatively smaller, as the pressure is distributed over the peripheral elastic elements of the system; but for a pulse duration of the order of 2 msec the core pressure still amounts to a sizeable part of the peripheral one. Only starting with the static phase of compression is the fall in core pressure so abrupt and pronounced.

The compression which gave rise to the generator potential of the experiment illustrated in Fig. 12 is comparable in amplitude and velocity to that for which the core pressure was computed (Fig. 10). In the experiment, the compression is rounded at its peak; this will cause the core pressure to drop less steeply than in the computed case. But except for this difference, which amounts to less than a fraction of a millisecond in falling time of pressure, the pressure curve at the core in the experiment should correspond to that of Fig. 10. We may then try to see how well this

curve accords with that of the transduced current of the receptor. The generator potential, recorded extracellularly from the nerve fibre at a distance of about 800μ from the tip of the nerve ending, rises in 2 msec to peak and falls to zero with a time constant of 3–5 msec (Fig. 12). During the entire response, electrical charge is being passively redistributed over

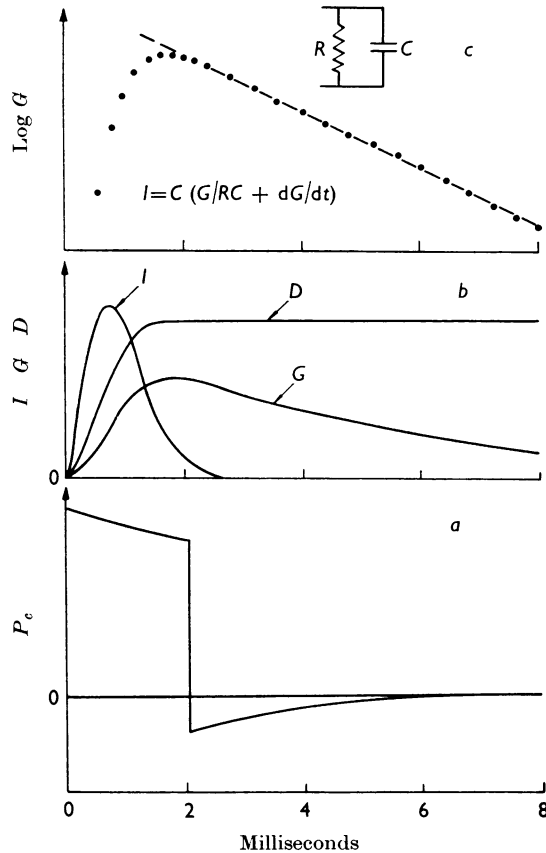


Fig. 12. Comparison between core pressure and transducer response. (a) Computed core pressure (P_c) resulting from an external lamella displacement of the kind illustrated in Fig. 10b.

(b) Generator response to a similar displacement in a Pacinian corpuscle. Displacement is produced by a piezo-electric crystal, and the resulting generator potential is recorded from the nerve fibre where it emerges from the corpuscle. D , tracing of photo-electric record of outer lamella displacement; G , tracing of generator potential; I , derived curve of generator current ('transducer action') as determined by equation shown in c, where the R-C combination is the lumped equivalent of the passive electrical components of the nerve fibre system in the corpuscle (see text for uncertainties).

(c) Determination of the duration of the 'transducer action' of generator response G . See text.

the capacitance of the nerve fibre membrane. On the assumption that the later part of the falling phase of the response represents passive charge transfer among the capacitative elements through the conductance of the system recovered to resting value, we may estimate the duration of the transducer action, i.e. of the active phase of the transducer current. This is considered as extending from the time of response onset until the time when the falling phase becomes a pure exponential decay (Fig. 12c). The duration of the transducer action may then be compared directly with that of the core pressure, its assumed precursor. The comparison is made in Fig. 12. The agreement between the two is very satisfying. Evidently, the mechanics of the corpuscle, i.e. the mechanical filter action of the lamellae, can alone account for the process of adaptation of the generator response.

Ideally one would like to compare the whole time course of the transducer action with that of the core pressure. An approximation of the time course of the transducer action may be obtained by differentiation of the generator potential with respect to time, and compensation for the passive decay of generator potential by adding to the derivative at each instant the corresponding value of the instantaneous generator potential divided by the time constant of the passive decay as applicable to a network of the kind illustrated in Fig. 12c, inset. Figure 12 gives the time course of the transducer action so obtained (I) and that of the core pressure (P_c) on the same time scale. It should be noted, however, that the validity of derivation of the whole time course of the transducer action is based on the validity of the assumption that the passive charge transfers during the transducer action are not themselves time-dependent in the excited membrane, i.e. that they are largely ruled by the time constants of the non-excited membrane. This is uncertain and, therefore, the precise shape of the derived I curve is uncertain. The terminal points of the curve, i.e. the duration, do not depend on these assumptions; and the main point here is the good correspondence between the duration of the transducer action and the duration of the core pressure. This correspondence alone warrants the above conclusion on generator response adaptation.

The filter action of the capsule is a sufficient factor in determining the rate of adaptation of the generator potential. But is it the only one, or is the duration of the generator potential itself also rate-limiting in adaptation? This question received recently a direct answer from experiments. In these experiments, the filter action of the peripheral lamellae was bypassed, and compression was applied rather directly to the core of corpuscles from which most of the lamellae outside the core had been dissected away. Under these conditions, the generator potential in response to compressions of the kind considered in Fig. 12 turned out to have durations of 70 msec, an order of magnitude longer than that in corpuscles with complete lamella filter equipment (Loewenstein & Mendelson, 1965). *Thus, clearly, the rate-limiting factor of the decay in generator potential to a sustained stimulus, that is, the rate-limiting factor of receptor adaptation, is the filter action of the capsule in the Pacinian corpuscle.*

The experiments on decapsulated corpuscles also confirm the validity

of some of the general theoretical concepts of the present analysis. To re-convert a decapsulated receptor preparation into a receptor of the fast-adapting kind, i.e. to obtain adequate mechanical filter action by enclosing the decapsulated core in an artificial lamellated capsule, the following conditions had to be met: (1) the artificial lamella had to be elastic, and (2) there had to be fluid in between them (Loewenstein & Mendelson, 1965).

Generator mechanisms of fast and slowly adapting receptors. A related question concerns the electrical generator mechanism as such. Are the electrical generator mechanisms of a fast-adapting receptor different from a slowly adapting one in regard to ability of maintaining a current output? Slowly adapting mechanoreceptors, such as the muscle spindle (Katz, 1950), slow crustacean stretch receptors (Eyzaguirre & Kuffler, 1955; Krnjević & van Gelder, 1961; Wendler & Burkhardt, 1961), bee hair-plate receptors (Thurm, 1964), can clearly hold an uninterrupted current output for seconds or minutes. In a fast-adapting receptor, such as the Pacinian corpuscle here, this point is not immediately clear, because the capabilities of the electrical generator in this respect are masked by mechanical filtering. However, in view of the prolongation in generator response in partially decapsulated corpuscles mentioned before and a number of other experimental observations in decapsulated corpuscles (Loewenstein & Mendelson, 1965), it seems likely that the generator capabilities of Pacinian corpuscles are essentially similar to those of slowly adapting receptors. (Capabilities for nerve impulse production, however, are markedly different.) Recent results obtained on fast and slowly adapting crustacean stretch receptors (Nakajima, 1964) lead to a similar conclusion.

Velocity dependence of the generator response. The primary elements of the capsule, as used in the present theory, are the lamellae, their radial connexions, and the fluid. The former two provide the structural elements and elastic forces for the filter action, and the latter, the viscous element for the dynamic transmission of forces. The lamellae operates like a series of dashpot pistons which, in displacing fluid, generate viscous pressure. The elastic connexions between pistons are so weak that only viscous pressure propagates to any significant extent through the capsule. Thus propagation of pressure through the capsule may be expected to be velocity-dependent. This explains the velocity dependence of the generator response (Gray & Sato, 1953; Álvarez-Buylla & Remolina, 1959).

Off-response

A striking feature of the behaviour of the Pacinian corpuscle is the second generator potential which ensues upon release of compression. This is the 'off-response' of the receptor which probably plays an important

role in the sensory coding of stimulus duration. The response has two paradoxical features: (i) it has the same polarity as the 'on-response'; and (ii) under certain conditions it may have a greater amplitude than the 'on-response'. Both are accounted for by the present analysis.

When the corpuscle is compressed to a steady level, static mechanical state is reached in about 15 msec. Figure 8 gives the final pressure distribution for a compression of 20μ . When compression is released, the energy stored in the elastic lamellae during compression is set free, and viscous pressure is developed again. It is easy to see that during release the resulting local lamellae velocities are reversed and the over-all pressure distribution is rotated by 90° with respect to those during compression. But such a rotation introduces no essential change in the mode of response of the transducer nerve ending. The transducer does not appear to discriminate direction of pressure applied. The polarity (and the order of magnitude) of the generator response to compression in one plane is the same as in another, as is readily verified experimentally by rotating a Pacinian corpuscle around its length axis and varying the angle of compression to a reference plane. Hence, the polarity of the generator response to release will be the same as that to compression.

The question then is whether the core pressure during release from compression is sufficient to account for the off-response. The analysis shows that during the dynamic phase of a release, the core pressure can, indeed, be of the same order as that during the dynamic phase of compression (Fig. 11).

A further interesting outcome of the analysis is that the peak pressure in a release can actually exceed that in a compression depending on the respective velocities. Figure 13 provides a numerical example and a summary of the relevant parameters. The rate of compression in the example is $10\mu/\text{msec}$, and the rate of release initially $12.6\mu/\text{msec}$, as determined by the passive mechanical constants of the corpuscle. The peak pressure resulting from release is greater than that resulting from compression in this case. The difference is due to the fact that the peak core pressure during compression is determined by the rate of compression, but is quite independent of the final force required to maintain static conditions; while the peak pressure developed during release depends primarily on this final force, which may be considerable. This provides a satisfactory explanation for the relative amplitudes of the experimental on- and off-responses illustrated in Fig. 13, inset.

The present theory attributes the off-response of the Pacinian corpuscle entirely to mechanical properties of its capsule. The immediate energy source of the response is assigned to the elastic lamellae, the storage elements for the energy supplied originally by the external stimulus

during compression. A simple test for the validity of these notions is provided by experiments on decapsulated corpuscles. After elimination of the lamellae outside the core, the off-response can no longer be elicited, although the on-response continues to be present (Loewenstein & Mendelson, 1965).

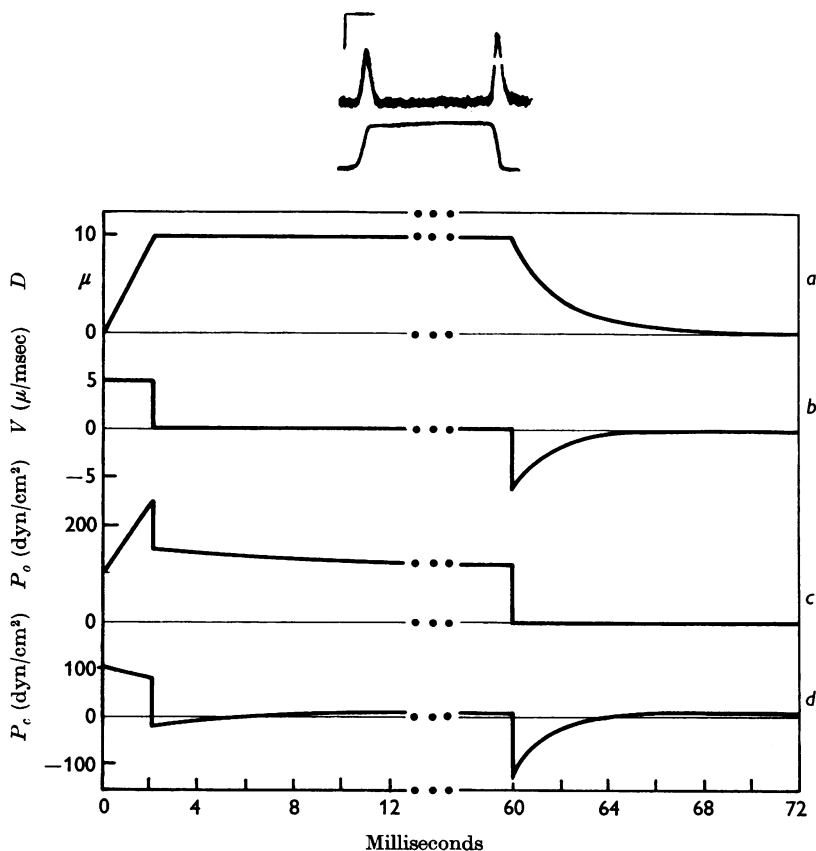


Fig. 13. Precursors of on- and off-responses. Time course of computed velocities and pressures under a compression of 20μ applied uniformly during 2 msec and released suddenly after 60 msec. Release is such that the restoration of the corpuscle to its normal uncompressed shape is controlled entirely by its passive mechanical constants. D , displacement of outer lamella (the stimulus). V , velocity of outer lamella. P_o , pressure on outer lamella. P_c , pressure on core.

Inset. On- and off-responses. Experimental generator potentials of a Pacinian corpuscle in response to compression and release of compression similar to those in D . The corpuscle is stimulated by the displacements of a piezo-electric crystal transmitted to the outer lamella by a rigid stylus. Upper beam, generator potential (calibration, 50μ); lower beam, photo-electric record of stylus displacement. Time calibration, 10 msec.

APPENDIX A

Compliance of a simply supported cylindrical membrane

Consider a single cylindrical membrane of length, b , and radius, a , with axis chosen as in Fig. 3 subject to the inward radial pressure, p

$$p = A \cos (2\theta) \cos \left(\pi \frac{x}{b} \right). \quad (\text{A } 1)$$

The equations of equilibrium of the membrane are (Timoshenko & Woinowsky-Krieger, 1959)

$$\frac{\partial N_x}{\partial x} + \frac{1}{a} \frac{\partial N_{x\theta}}{\partial \theta} = 0, \quad (\text{A } 2)$$

$$\frac{\partial N_{x\theta}}{\partial x} + \frac{1}{a} \frac{\partial N_\theta}{\partial \theta} = 0, \quad (\text{A } 3)$$

$$N_\theta = -pa \quad (\text{A } 4)$$

where

N_x = tension per unit length in the membrane in the x direction, dyn/cm,

N_θ = tension per unit length in the membrane in the θ direction, dyn/cm,

$N_{x\theta}$ = shear force per unit length in membrane in x and θ directions, dyn/cm.

From eqns. (A 1) and (A 4):

$$N_\theta = -Aa \cos (2\theta) \cos \left(\pi \frac{x}{b} \right). \quad (\text{A } 5)$$

Substituting eqn. (A 5) into (A 3) and integrating yields

$$N_{x\theta} = -2A \frac{b}{\pi} \sin (2\theta) \sin \left(\pi \frac{x}{b} \right). \quad (\text{A } 6)$$

Similarly, substituting eqn. (A 6) in (A 2) and integrating yields

$$N_x = A \frac{4b^2}{a\pi^2} \cos (2\theta) \cos \left(\pi \frac{x}{b} \right). \quad (\text{A } 7)$$

Two constants of integration not shown in eqns. (A 6) and (A 7) have been taken equal to zero to satisfy the boundary condition associated with the assumption of a simply supported boundary, namely, $N_x = 0$ at $x = \pm \frac{1}{2}b$.

Now the strains ϵ_x and ϵ_θ in the x and θ directions, and the shear strain, $\gamma_{x\theta}$, may be expressed in terms of the stresses N_x , N_θ , $N_{x\theta}$ and also in terms of the displacements u , v , w in the x , θ and r directions, respectively. The displacements are hence related to the stresses as follows (Timoshenko & Woinowsky-Krieger, 1959):

$$\epsilon_x = \frac{\partial u}{\partial x} = \frac{1}{Ed} (N_x - \nu N_\theta), \quad (\text{A } 8)$$

$$\epsilon_\theta = \frac{1}{a} \frac{\partial v}{\partial \theta} - \frac{w}{a} = \frac{1}{Ed} (N_\theta - \nu N_x), \quad (\text{A } 9)$$

$$\gamma_{x\theta} = \frac{1}{a} \frac{\partial u}{\partial \theta} + \frac{\partial v}{\partial x} = \frac{2(1+\nu)}{Ed} N_{x\theta}, \quad (\text{A } 10)$$

where d = thickness of the membrane, cm,

E = Young's modulus, dyn/cm²,

ν = Poisson's ratio.

Equations (A 8), (A 9) and (A 10) can be integrated to yield expressions for the displacements u , v , w after substituting eqns. (A 5), (A 6) and (A 7) for N_x , N_θ and $N_{x\theta}$. The results are:

$$u = -\frac{bAa}{\pi Ed} \left(\frac{4b^2}{\pi^2 a^2} - \nu \right) \cos(2\theta) \sin\left(\pi \frac{x}{b}\right) \quad (\text{A } 11)$$

$$v = \frac{2b^2 A}{\pi^2 Ed} \left(2 + \nu \frac{4b^2}{\pi^2 a^2} \right) \sin(2\theta) \cos\left(\pi \frac{x}{b}\right), \quad (\text{A } 12)$$

$$w = \frac{Aa^2}{Ed} \left(1 + \frac{4b^2}{\pi^2 a^2} \right)^2 \cos(2\theta) \cos\left(\pi \frac{x}{b}\right). \quad (\text{A } 13)$$

Equations (A 13) and (A 1) give directly the formulas expressed by eqns. (3) and (4) in the body of the paper.

APPENDIX B

Viscous fluid resistance to flow between two cylindrical membranes

Consider a rigid solid cylinder of radius, a , and length, b , with axes as shown in Fig. 3 surrounded by a cylindrical membrane of radius, $a + h$, and length, b , where h is small compared to a , so that a thin cylindrical space is formed between the membrane and the solid cylinder. This space is assumed to be filled by an incompressible viscous liquid and the ends of the space are considered to be sealed against leakage by fixed end plates. Any motion of the membrane must be such that its total enclosed volume is constant, and the fluid must flow from one part of the space to another. This flow takes place through the narrow space of height, h , and may be categorized as a viscous flow. It will be shown that the expected Reynolds numbers are small.

If the space height, h , is sufficiently small compared to the radius, a , the curvature of the cylinder may be neglected in computing the velocity distribution in the fluid, by a reasoning similar to that commonly employed in boundary layer and lubrication theory (Pai, 1956). The flow requires a

pressure field, p , and, under the assumption of a viscous flow at low Reynolds number, the equations of motion of fluid reduce to (Pai, 1956, p. 128)

$$\frac{\partial p}{\partial x} = \mu \frac{\partial^2 v_x}{\partial r^2}, \quad (\text{B } 1)$$

$$\frac{\partial p}{\partial s} = \mu \frac{\partial^2 v_\theta}{\partial r^2}, \quad (\text{B } 2)$$

where v_x and v_θ are the components of velocity in the x and θ directions, μ is the viscosity of the fluid, dyn sec/cm², and s is equal to $a\theta$. Under the assumptions made, p will be independent of r ; with the boundary conditions

$$v_x = v_\theta = 0 \quad \text{at} \quad r = a \quad \text{and} \quad r = a + h, \quad (\text{B } 3)$$

Equations (B 1) and (B 2) may be integrated to yield

$$Q_x = -\frac{h^3}{12\mu} \frac{\partial p}{\partial x}, \quad (\text{B } 4)$$

$$Q_s = -\frac{h^3}{12\mu} \frac{\partial p}{\partial s}, \quad (\text{B } 5)$$

where Q_x and Q_s are the discharges per unit length (cm²/sec) in the x and s directions, respectively, defined by

$$Q_x = \int_a^{a+h} v_x dr \quad (\text{B } 6)$$

$$Q_s = \int_a^{a+h} v_\theta dr \quad (\text{B } 7)$$

The velocity profiles are parabolic, as may be expected in a laminar flow.

Now consider the equation of continuity or conservation of mass (Pai, 1956, p. 38)

$$\frac{\partial v_x}{\partial x} + \frac{\partial v_\theta}{\partial s} + \frac{\partial v_r}{\partial r} + \frac{v_r}{r} = 0, \quad (\text{B } 8)$$

where v_r is the radial velocity of the fluid, taken positive in the increasing r direction. In terms of the membrane displacement w , the radial velocity at $r = a + h$ is

$$(v_r)_{r=a+h} = -\dot{w}, \quad (\text{B } 9)$$

where the dot stands for differentiation with respect to time and w is measured positive inwards. Integrating eqn. (B 8) with respect to r from a to $(a + h)$ yields the equation of continuity in the present approximation as

$$\frac{\partial Q_x}{\partial x} + \frac{\partial Q_s}{\partial s} = \dot{w} \quad (\text{B } 10)$$

Substituting the viscous equations (B 4) and (B 5) in eqn. (B 10) gives

$$-\frac{h^3}{12\mu} \left(\frac{\partial^2 p}{\partial x^2} + \frac{\partial^2 p}{\partial s^2} \right) = \dot{w}. \quad (\text{B } 11)$$

Next suppose that w has the form of the membrane deflexion

$$w = B \cos (2\theta) \cos \left(\pi \frac{x}{b} \right), \quad (\text{B } 12)$$

where B is a function of time. Equation (B 11) becomes an equation for the pressure, p

$$-\frac{h^3}{12\mu} \left(\frac{\partial^2 p}{\partial x^2} + \frac{1}{a^2} \frac{\partial^2 p}{\partial \theta^2} \right) = \dot{B} \cos (2\theta) \cos \left(\pi \frac{x}{b} \right), \quad (\text{B } 13)$$

where s has been replaced by $a\theta$. The appropriate solution for p which satisfies eqn. (B 13) is

$$p = \frac{12\mu b^2 \dot{B}}{h^3 \pi^2 (1 + 4b^2/\pi^2 a^2)} \cos (2\theta) \cos \left(\pi \frac{x}{b} \right). \quad (\text{B } 14)$$

Equations (B 14) and (B 12) lead to the interpretation given in eqns. (3), (8), (9) and (10) in the body of the paper. In the above derivation only one boundary of the fluid is considered movable for convenience. If the other boundary were to move, a similar derivation applies and the relative motion controls the net viscous pressure, as indicated in the body of the paper.

As a rough check on the Reynolds numbers of the flows to be expected, assume the fluid velocities involved to be of the order of magnitude of the velocities of compression used typically in experiments. From data given by Hubbard (1958), a velocity of $35 \mu/\text{msec}$ (3.5 cm/sec) is typical. The largest spacing of lamellae is about 25μ ($25 \times 10^{-4} \text{ cm}$). Then the typical Reynolds number of the flow is

$$R_N = \frac{Vh}{\nu} = \frac{3.5(25 \times 10^{-4})}{0.01} = 0.875, \quad (\text{B } 15)$$

where ν is the kinematic viscosity assumed equal to 1 centistoke. The Reynolds number is sufficiently small to justify the assumption of linearity of the equation and to neglect acceleration.

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